Characteristics of Plant Stoichiometric Homeostasis (Postprint)

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Abstract

Stoichiometric homeostasis is one of the core concepts in ecological stoichiometry research, referring to the ability of organisms to maintain relatively stable chemical composition when facing external changes, which reflects the physiological and biochemical responses and adaptations of organisms to environmental changes. Based on the determination of N, P and other element contents in soil and plants, the plant homeostasis index (H) can be estimated. Generally, plant stoichiometric homeostasis is weaker than that of animals, and the variation range of homeostasis is relatively large. Stoichiometric homeostasis is an important mechanism for maintaining ecosystem structure, function, and stability; species with high homeostasis have higher dominance and biomass stability, while ecosystems with high homeostasis have higher productivity and stability. Therefore, homeostasis is considered an important indicator for measuring species competitiveness. Studying plant ecological stoichiometric homeostasis helps to deeply understand plant adaptation strategies and ecological adaptability to the environment, as well as the relationship between plant stoichiometric homeostasis and ecosystem function. However, current research on plant ecological stoichiometric homeostasis is relatively limited. Existing studies have shown that different species or functional groups have different ecological stoichiometric homeostasis characteristics due to their different growth strategies; there are significant differences in homeostasis among different organs, different growth stages, and different elements of the same species. This paper reviews the concept of plant ecological stoichiometric homeostasis, calculation methods for the homeostasis index H, homeostasis characteristics of different plant species or functional groups, different organs, and different growth stages, as well as the relationship between plant homeostasis and ecosystem structure, function, and stability. Combined with work already carried out, it provides prospects for research areas related to plant ecological stoichiometric homeostasis that need further expansion, with the aim of providing references for promoting the

development of related domestic research work.

Full Text

Preamble

Characteristics of Plant Ecological Stoichiometry Homeostasis

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Abstract

Stoichiometric homeostasis is one of the core concepts in ecological stoichiometry, referring to the ability of organisms to maintain relatively stable chemical composition in response to environmental variation. This capacity reflects the physiological and biochemical responses and adaptations of organisms to surrounding environmental changes. Based on measurements of nitrogen (N), phosphorus (P), and other element contents in soils and plants, plant homeostatic indices (H) can be estimated. Generally, plant stoichiometric homeostasis is weaker than that of animals and exhibits greater variation. Stoichiometric homeostasis represents an important mechanism for maintaining ecosystem structure, function, and stability. Species with high homeostasis tend to have greater dominance and biomass stability, while ecosystems dominated by such species exhibit higher productivity and stability. Consequently, homeostasis is considered a crucial indicator of species competitiveness. Investigating plant ecological stoichiometric homeostasis enhances our understanding of plant adaptation strategies and ecological adaptability, as well as the relationship between plant stoichiometric homeostasis and ecosystem functions. However, current research on plant ecological stoichiometric homeostasis remains limited. Existing studies indicate that different species or functional groups possess distinct ecological stoichiometric homeostasis characteristics due to varying growth strategies, and substantial differences exist in homeostasis among different organs, growth stages, and elements within the same species. This paper reviews the concept of plant ecological stoichiometric homeostasis, methods for calculating the homeostatic index H, homeostasis characteristics across different plant species or functional groups, organs, growth stages, and elements, and the relationship between plant homeostasis and ecosystem structure, function, and stability. Based on current achievements and ongoing research, we propose perspectives for future studies in plant ecological stoichiometric homeostasis to promote the development of related research in China.

Keywords: ecological stoichiometry, homeostasis, plant, ecosystem stability

1. Concept and Principles of Ecological Stoichiometric Homeostasis

Homeostasis theory describes the ability of organisms to maintain relatively stable stoichiometric characteristics when facing changes in elemental availability in the external environment (Sterner & Elser, 2002). Through long-term evolutionary processes, organisms maintain relatively stable internal chemical composition via dynamic equilibrium, keeping internal environmental variation within a narrow range and establishing internal homeostatic mechanisms (Sterner & Elser, 2002; Zhang, 2003). This capacity to maintain stable chemical composition formed through long-term adaptation to environmental changes is termed ecological stoichiometric homeostasis (hereafter referred to as homeostasis) (Kooijman, 1995; Jiang et al., 2017). The principle of dynamic equilibrium in organismal chemical composition forms the theoretical foundation of ecological stoichiometry. In biology, dynamic equilibrium maintains internal nutrient balance, pH, and other parameters relatively constant despite external environmental fluctuations, and is thus considered an essential characteristic of life (Zeng & Chen, 2005). In ecological stoichiometry, elemental dynamic equilibrium refers to a state where organismal elemental composition remains relatively stable relative to the surrounding environment, available resources, and nutrient supply, serving as the theoretical basis for ecological stoichiometry (Sterner & Elser, 2002).

Plant ecological stoichiometric homeostasis characteristics result from long-term evolutionary adaptation to the environment. When confronted with environmental changes, plants maintain stable elemental characteristics through biochemical, physiological, and ecological processes (Sterner & Elser, 2002; Jiang et al., 2014). When a particular element limits plant growth, plants can alter the availability and utilization efficiency of that element through various physiological and biochemical mechanisms to maintain stable nutrient content and related traits (Hessen et al., 2004). Elemental uptake is regulated not only by the storage level of that element within the plant but also by the content of other elements. For example, plants reduce NO_3^- absorption when cellular C and N contents are high or P content is low (Chapin, 1991; Grossman & Takahashi, 2001; Frost et al., 2005). Carbon, nitrogen, and phosphorus are primary life elements and fundamental components of organisms; therefore, homeostasis characteristics in ecological stoichiometry mainly refer to the stability of C, N, and P contents and their ratios (Tang & Dam, 1999; Sterner & Elser, 2002; Su, 2012).

Organisms comprise various compounds, each with specific elemental compositions and ratios. Additionally, organisms contain numerous free ions, and plants absorb nutrient elements in ionic form. Consequently, organismal elemental composition and ratios are influenced by environmental elemental composition. If the variation in elemental content and ratios within an organism perfectly matches that of the external environment, the organism is considered non-homeostatic, exhibiting a positive correlation with a slope of 1 (Fig. 1

[Figure 1: see original paper]A). If an organism' s stoichiometric characteristics are independent of environmental resource stoichiometry, the relationship curve has a slope of 0 (Fig. 1B), representing strict homeostasis. However, absolute non-homeostasis and absolute homeostasis do not exist in reality, as organismal elemental content variation has certain limits (Su, 2012).

Note: The abscissa indicates stoichiometric characteristics of external environmental resources, such as P%, N%, or N:P, while the ordinate indicates stoichiometric characteristics of organisms. The dashed line in Fig. 1A shows organism stoichiometric characteristics changing completely with the external environment, with solid lines indicating continuous environmental influence. The solid line in Fig. 1B represents organism stoichiometric characteristics independent of the external environment, showing strict homeostasis.

Fig. 1 Relationship between elemental concentrations in environment and organisms (Sterner & Elser, 2002)

Ecological stoichiometric homeostasis is a quantifiable parameter. Sterner & Elser (2002) proposed a biological ecological stoichiometric homeostasis model expressing the relationship between organismal and environmental stoichiometric characteristics as:

$$y = c \cdot x^{1/H}$$

where x represents nutrient supply in the environment, y represents elemental content in the organism, and both x and y are concentration percentages or elemental ratios, such as P%, N%, or N:P. Expressing this formula in exponential form yields:

$$y = c \cdot x^{1/H}$$

where c is a constant. Logarithmic transformation of both sides allows the relationship between x and y to be expressed as:

$$\log(y) = \log(c) + \frac{1}{H}\log(x)$$

Thus, the homeostatic index H can be expressed as:

$$H = \frac{\log(x)}{\log(y) - \log(c)}$$

In this model, $H > 1$ is considered indicative of homeostatic capacity (Sterner & Elser, 2002). For statistical convenience, $1/H$ ($0 < 1/H < 1$) is often used to measure homeostasis strength (Hood & Sterner, 2010). Persson et al. (2010) categorized $1/H$ into four types: $0 < 1/H < 0.25$ (homeostatic), $0.25 < 1/H <$

0.5 (weakly homeostatic), $0.5 < 1/H < 0.75$ (weakly plastic), and $1/H > 0.75$ (plastic). However, in vascular plant homeostasis studies, some scholars directly calculate H values to characterize homeostasis magnitude (Yu et al., 2010, 2011, 2015; Li et al., 2016). Yu et al. (2010) suggested that the ecological stoichiometric homeostasis index H can predict various intrinsic organismal characteristics, such as physiological regulation capacity in response to abiotic factors.

Although the stoichiometric homeostasis index plays an important role in predicting species' roles in population dynamics, food webs, and nutrient cycling, cautious application and interpretation of the parameter $1/H$ are necessary both physiologically and statistically. The relationship between $1/H$ and consumer stoichiometric homeostasis regulation is exponential rather than linear, and categorizing $1/H$ into several classes may oversimplify the measurement of stoichiometric homeostasis (Persson et al., 2010). When environmental stoichiometric characteristics vary greatly while consumer stoichiometry is strongly constrained or varies independently of the environment, the homeostasis index may not accurately reflect consumer homeostasis. Furthermore, some scholars have calculated negative stoichiometric homeostasis indices for organisms through field studies (Persson et al., 2010; Xing et al., 2015), generally using the absolute value of H to characterize the strength of biological stoichiometric homeostasis.

2. Characteristics of Plant Ecological Stoichiometric Homeostasis

Homeostasis is an essential characteristic of organisms, including stability of pH, water content, and other parameters. Ecological stoichiometric homeostasis primarily refers to the stability of elemental composition and ratios. Plant elemental composition stability is mainly regulated by fundamental physiological processes such as nutrient uptake, assimilation, and utilization (Sterner & Elser, 2002). Due to varying nutrient demands at different growth stages, plant homeostatic indices show considerable variation across developmental phases. The homeostasis index not only reflects plant stability characteristics and environmental adaptation strategies but also serves as an important parameter indicating ecosystem stability and productivity (Yu et al., 2010). Plants with strong homeostasis tend to have more conservative nutrient utilization strategies, maintaining slow growth even in nutrient-poor environments, while plants with weaker stability exhibit greater adaptability (Persson et al., 2010). Consequently, homeostatic plants may be better adapted to stable environments, whereas plants with lower homeostatic indices may have advantages in variable environments. Although the stoichiometric homeostasis index H is an important parameter in ecological stoichiometry, quantitative data on plant ecological stoichiometric homeostasis indices remain scarce (Zeng et al., 2013). Analysis of currently limited literature reveals substantial variation in ecological stoichiometric homeostasis indices across different plant species or functional groups, growth stages, and organs or tissues. Therefore, we provide a brief review of plant ecological stoichiometric homeostasis characteristics from these perspectives.

2.1 Stoichiometric Homeostasis Characteristics of Different Species and Functional Groups

Different species or functional groups exhibit significant differences in processes of chemical element absorption, transport, allocation, utilization, and release (Yan et al., 2013; Sistla et al., 2015). Various plant species or functional groups employ different ecological adaptation strategies (Güsewell, 2004), adjusting their elemental contents and ratios through physiological and ecological processes to adapt to the environment. Consequently, different species or functional groups may possess distinct stoichiometric homeostasis characteristics (Table 1). Persson et al. (2010) found that among 20 algal species, some exhibited strict stoichiometric homeostasis while others showed weaker homeostatic capacity. Yu et al. (2010) conducted field N and P addition experiments on 12 species in Inner Mongolia grasslands, revealing that plant homeostasis indices positively correlated with species dominance—dominant species had higher homeostatic indices than other species. They suggested that species with high homeostasis indices may employ more conservative nutrient utilization strategies, enabling them to better adapt to the nutrient-poor grassland environment and become dominant species. Under P addition conditions, both biomass and P homeostasis indices of grasses in subalpine meadows were higher than those of legumes, sedges, and other forbs, possibly due to grasses' well-developed root systems enabling rapid nutrient uptake. Higher P homeostasis also significantly influenced grass competitiveness (Zhang et al., 2015). In aquatic ecosystems, macrophytes showed smaller elemental variation ranges than algae, indicating higher stoichiometric homeostasis in macrophytes (Cross et al., 2005; Demars & Edwards, 2007; Tsoi et al., 2011; Feijoó et al., 2014). Shrubs and mosses exhibited different stoichiometric homeostasis characteristics in fertilization experiments, with mosses showing weaker N homeostasis but stronger P homeostasis than shrubs (Wang et al., 2016). Luo (2017) found that wheat, maize, and cotton in oasis farmland ecosystems showed significantly different trends in homeostasis indices during plant development. Leguminous shrubs exhibited low dependence on environmental N, with higher N content and N:P ratios than non-leguminous shrubs. Compared with leguminous shrubs, non-leguminous shrubs showed stronger correlations between leaf N content and soil N content, indicating that leguminous shrubs have higher N homeostasis (Guo et al., 2017). Invasive plants demonstrate higher homeostasis than native plants, and this elevated homeostasis may contribute to invasion success (Jiang et al., 2014, 2017).

Table 1 Ecological stoichiometric homeostasis values of different species and functional groups

Species/Functional Group	Stoichiometric Homeostasis Values	References
Daphnia	2.04–3.45	(DeMott & Pape, 2005; Yu et al., 2011)
Shrub	1.3–2.33	(Guo et al., 2017)
Desert plant	(Zhang et al., 2017)	
Chinese herb	3.54–7.68	
American herb	3.87–5.60	(Yu et al., 2011)
Tundra vascular plant	3.15–10.29	(Yu et al., 2011)
Wetland plant	4.30–9.60	(Dijkstra et al., 2012)
Aquatic plant	2.70–7.10	
Chlorophyte	1.60–2.90	(Gu et al., 2017)
Evergreen forest seedling	2.30–5.40	
Arabidopsis thaliana	1.40–2.02	(Jiang et al., 2014)
Suaeda heteroptera	3.30–5.24	(Jiang et al., 2014)
Triticum aestivum	3.52–4.03	(Jiang et al., 2014)
Zea mays	3.58–13.91	(Luo et al., 2017)
Anemone vitifolia	6.19–22.58	(Luo et al., 2017)
Amaranthus ascendens	5.10–20.35	(Luo et al., 2017)
Grass	3.00–4.80	(Peng et al., 2016)
Carex curta	2.20–7.10	(Ryser & Lambers, 1995; Elser et al., 2010)
Subtropical forest	2.50–2.90	(Güsewell, 2004)

2.2 Stoichiometric Homeostasis Characteristics at Different Plant Growth Stages

Plant ecological stoichiometric homeostasis varies with developmental processes, and different species may show different trends due to distinct growth strategies.

Additionally, because different organs perform different functions, homeostasis trends may differ among organs within the same species. Yu et al. (2011) studied three herbaceous species (*Leymus chinensis*, *Chenopodium glaucum*, and *Cleistogenes squarrosa*), finding that homeostasis indices for leaf N (H), P (H), and N:P ratio (H :) all increased with the growing season, indicating a positive relationship between leaf homeostasis index and growth stage. This suggests that as plant regulatory systems mature, their response to environmental nutrient variation gradually weakens. Because different elements serve different functions within plants, N and P show different trends during plant development (Peng et al., 2016). In wetland ecosystems, organ-specific homeostasis indices vary across developmental stages. With plant growth, H , H , and H : in roots of *Spartina alterniflora* decreased, as did H and H : in roots and stems and H : in roots of *Phragmites australis* and *Cyperus malaccensis* var. *brevifolius*. In contrast, H and H : in stems and leaves of *S. alterniflora*, H and H : in leaves of *P. australis*, and H : in stems of *C. malaccensis* var. *brevifolius* showed increasing trends. These patterns reflect trade-offs in nutrient allocation between aboveground and belowground organs during growth in nutrient-limited environments and represent long-term adaptive responses (Jiang et al., 2014). Peng et al. (2016) investigated homeostasis indices for N and P at different growth stages of *Amaranthus mangostanus*, finding leaf H values of 4.76, 3.03, and 4.35 at seedling, flowering, and seed-filling stages, respectively, while H peaked at flowering (7.14) after being 2.17 at the seedling stage. They suggested that N regulates organ formation, with higher N homeostasis during growth than reproductive stages, while elevated P homeostasis during reproduction reflects the need for stable P supply to maintain reproductive growth.

2.3 Stoichiometric Homeostasis Characteristics of Different Plant Organs

Because different plant organs perform distinct functions, different organs within the same organism exhibit different homeostasis characteristics. In Inner Mongolia grasslands, belowground homeostasis indices of vascular plants negatively correlated with aboveground indices, reflecting different growth strategies for adapting to nutrient-poor environments through differential organ nutrient allocation. For example, the dominant species *Leymus chinensis* maintains high aboveground homeostasis through nutrient absorption and storage by its less-homeostatic belowground parts, enabling stable plant growth (Yu et al., 2011). In degraded grasslands of northeastern China, root homeostasis indices for N and P in *L. chinensis* were higher than those in leaves (Li et al., 2016). In wetland ecosystems, root H in *S. alterniflora* and *C. malaccensis* var. *brevifolius* was significantly higher than in stems, while sheath H : was significantly higher than in roots (Jiang et al., 2017). Studies on tree seedlings and shrubs also found higher stoichiometric homeostasis in leaves than in roots (Garrish et al., 2010; Minden & Kleyer, 2014; Schreeg et al., 2014). Our research on two dominant seedlings (*Symplocos ramosissima* and *Machilus gamblei*) in a mid-montane moist evergreen broad-leaved forest in Ailao Mountains, Yunnan, showed that leaf N homeostasis was lower than in stems and roots. Moreover, stem and leaf N homeostasis in *S. ramosissima* was higher than in *M. gamblei*, while root N homeostasis was lower (Fig. 2 [Figure 2: see original paper]), indicating that leaves are more sensitive to N input than roots and stems (Shi et al., 2015). These results demonstrate that aboveground and belowground elemental homeostasis show opposite trends, with plants adapting to environmental conditions and meeting growth requirements by adjusting nutrient allocation and utilization patterns among different organs.

Fig. 2 N homeostasis index in different organs of two seedlings in the N addition experiment (Shi et al., 2015)

2.4 Stoichiometric Homeostasis Characteristics of Different Elements

Carbon, nitrogen, and phosphorus are essential macronutrients for plant growth and development, with different elements performing different functions that lead to variations in content and homeostasis characteristics. In plankton, elements present at higher concentrations show stronger homeostasis than those at lower concentrations (e.g., N homeostasis > P homeostasis), and trace elements show weaker homeostasis than major elements (Karimi & Folt, 2006; Han et al., 2011). Current research on different plant groups largely supports this pattern. For instance, in Inner Mongolia grassland vascular plants, both aboveground and belowground H were higher than H , indicating stronger regulatory capacity for N, the more abundant element (Yu et al., 2011). In *Stipa bungeana*, C content showed low variation (coefficient of variation = 3.65%), indicating strong homeostasis, while N and P contents showed high variation (>30%), indicating weak homeostasis (Niu et al., 2011). In flue-cured tobacco at different developmental stages, C content showed the smallest variation coefficient and highest homeostasis (Yang et al., 2015). In degraded grasslands of northeastern China, leaf H in the dominant species *L. chinensis* was greater than H (Li et al., 2016). In wetland plants, N homeostasis indices were higher than P homeostasis indices (Jiang et al., 2017).

Additionally, studies show that plant N and P homeostasis indices (H , H) are typically smaller than H : because N and P accumulation in plant tissues is synergistic—N accumulation is usually accompanied by increased P content (Sterner & Elser, 2002). Compared with H and H , H : is less affected by external environmental factors and more strongly correlated with plant intrinsic properties, suggesting that plant homeostasis regulation is primarily manifested in N:P ratios rather than individual element contents (Zhao et al., 2011). Therefore, H : may better represent a plant' s true capacity to maintain homeostasis when assessing homeostasis strength.

3. Relationship Between Plant Ecological Stoichiometric Homeostasis and Ecosystem Structure, Function, and Stability

Ecological stoichiometric homeostasis serves not only as a tool for examining organism-environment relationships but also as an important indicator for assessing species richness and ecosystem structure, function, and stability (Sterner & Elser, 2002; Yu et al., 2010). Dominant species in plant communities exhibit higher homeostasis than other species, with homeostasis magnitude related to plant adaptation strategies and environmental adaptability. Plant nutrient utilization strategies are key factors regulating biodiversity and ecosystem structure, function, and stability. Ecosystems dominated by homeostatic species show higher productivity, suggesting that plant ecological stoichiometric homeostasis may be an important mechanism for maintaining ecosystem structure and stability (Yu et al., 2010). In grassland ecosystems, species with high N:P ratios have higher homeostasis indices, and homeostatic species maintain higher and more stable biomass. Ecosystems dominated by highly homeostatic species exhibit greater productivity and stability, indicating that stoichiometric homeostasis may be a crucial mechanism for maintaining grassland ecosystem structure, function, and stability (Yu et al., 2010, 2011).

Yu et al. (2010) conducted a two-year field fertilization experiment, 27-year monitoring, and 1200 km spatial gradient survey in Inner Mongolia grassland ecosystems. At the species level, leaf H showed strong positive correlations with species richness and stability across short-term, long-term, and spatial gradient experiments, while H showed poor correlations with species richness and stability, suggesting that grassland ecosystems are primarily N-limited. At the community level, community H values positively correlated with community stability and productivity in both two-year field experiments and 27-year monitoring, but this relationship only appeared in meadow steppe along the 1200 km spatial gradient, not in typical steppe or desert steppe. Bai et al. (2010) found that after four years of N addition in Inner Mongolia grasslands, species with high ecosystem homeostasis maintained higher biomass. In U.S. grasslands dominated by C_4 plants, nine years of N addition decreased abundance of species with high H and increased abundance of species with low H , with H accurately predicting species responses to N addition. In climate change experiments simulating water variation, species with highest N homeostasis showed greater stability and minimal response to soil moisture changes, while species with low N homeostasis were more sensitive to water changes. The positive correlation between H and species dominance was unaffected by water variation (Yu et al., 2015), indicating that highly homeostatic plant species are relatively less sensitive to water changes.

Our previous research on epiphytic mosses in Ailao Mountains, Yunnan, found that epiphytic mosses are highly sensitive to N deposition and air humidity changes, primarily because they lack roots and absorb nutrients and water directly from the atmosphere, making them effective bioindicators for environmental monitoring (Song et al., 2012a, 2012b). Additionally, our study on the facultative epiphytic fern *Selliguea griffithiana* showed significant plastic changes in morphological and physiological traits between epiphytic and terrestrial individuals. Epiphytic individuals' trait plasticity alleviated negative effects of water deficit, while terrestrial individuals' traits mitigated low light stress in forest understories (Lu et al., 2015). We therefore hypothesize that epiphytic plants may have lower stoichiometric homeostasis and weaker community structural stability. We are currently conducting related experimental research to explore the ecological stoichiometric characteristics of forest epiphytic plants independent of soil substrate nutrient influence.

Highly homeostatic species exhibit greater stability and dominance and may enhance ecosystem resistance stability, while low-homeostasis species affect ecosystem stability maintenance capacity. Li et al. (2016) demonstrated that high homeostasis in grassland dominant species plays an important role in maintaining grassland ecosystem stability, with degraded grassland soils showing significantly reduced C, N, and P contents. In grassland ecosystems, species with high H show higher stability and abundance than those with low H , and H may predict species abundance and stability and how plant species and ecosystems will respond to global change-induced alterations in resource availability (Yu et al., 2015). However, whether such predictions can be extended to other life forms or ecosystems (e.g., deserts, forests, wetlands) requires further investigation.

4. Factors Influencing Plant Ecological Stoichiometric Homeostasis

As homeostasis is formed through long-term environmental adaptation during plant evolution (Elser et al., 2010), current research on factors influencing plant homeostasis has focused primarily on intrinsic plant factors, with limited studies on external factors such as global climate change (e.g., warming, elevated CO_2, N and P deposition) and anthropogenic disturbances (e.g., fertilization, grazing, land use change, fire). Existing studies show that global change and anthropogenic activities alter species dominance by changing soil N and P contents, thereby affecting community and ecosystem structure and productivity (Güsewell, 2004). However, whether changes in external environmental factors cause alterations in plant homeostasis remains unreported and requires strengthened research.

Nutrient element contents in plant communities change during different successional stages. Yan et al. (2015) studied the pioneer species *Pinus massoniana* during subtropical forest succession, finding that in early successional stages with low soil N content, *P. massoniana* with high H better adapted to the environment and became dominant. As forest ecosystem succession progressed and soil N content increased, N-preferring broadleaf species absorbed and accumulated large amounts of N and P, causing significant reductions in soil P, especially available P, and decreasing dominance of *P. massoniana* with low P homeostasis. Yu et al. (2011) conducted a two-year field fertilization experiment in Inner Mongolia grasslands, finding that despite significant differences in rainfall between 2006 and 2007 (304 mm vs. 240 mm), homeostasis of three plant species (*L. chinensis*, *C. squarrosa*, and *C. glaucum*) showed no significant changes (P = 0.97). Yu et al. (2015) found that in U.S. grassland ecosystems, species stability relationships remained unchanged under N addition and altered water availability. We can therefore hypothesize that homeostasis is a fundamental plant attribute, particularly for highly homeostatic species, and may be less affected by external environmental changes such as precipitation and N deposition.

5. Research Perspectives

Academic attention analysis of literature and materials related to "stoichiometric homeostasis" searched in CNKI, Web of Science, and other databases shows that international research on stoichiometric homeostasis began earlier but focused primarily on animals, with limited plant research and few related publications. Although China' s attention to plant stoichiometric homeostasis has slowly increased since 2014, the number of published papers remains small. Currently, China' s research attention on plant ecological stoichiometric homeostasis is not high, and research achievements are limited.

Plant homeostasis is closely related to environmental adaptation strategies, community composition, structure, ecosystem stability, and productivity (Yu et al., 2010). As the main component of terrestrial ecosystems, plants provide energy directly or indirectly to consumers at all trophic levels and represent a critical link in ecosystem material cycling and energy flow. Human activity-induced global climate and environmental changes, N deposition, and other factors significantly affect plant growth and development, species composition, biodiversity and distribution, and productivity, causing changes in plant community composition and structure and intensifying ecosystem fluctuations (Elser et al., 2010). Ecological stoichiometric homeostasis studies plant stability from a nutrient element perspective and its relationships with community structure, ecosystem function and stability, and productivity, as well as plant homeostasis responses to N deposition, providing new entry points for ecological research. Therefore, strengthening research on plant stoichiometric homeostasis is crucial. Based on the current status of plant ecological stoichiometric homeostasis research in China, we recommend in-depth investigation of the following aspects in future studies:

(1) **Relationship between plant stoichiometric homeostasis characteristics and ecosystem structural stability and productivity.** While extensive research has examined how plant C, N, and P contents and N:P stoichiometric characteristics and environmental element contents affect plant growth and development (Wright et al., 2004; Han et al., 2005), studies on plant stoichiometric homeostasis remain limited, with existing research primarily at the species level and rare investigations of relationships between plant homeostasis and communities or ecosystems.

Some scholars suggest that plant stoichiometric homeostasis strength positively correlates with plant dominance and may affect ecosystem structure and productivity (Yu et al., 2010). However, Dijkstra et al. (2012) found that one of three dominant species in semiarid U.S. grasslands showed large N:P variation and weak homeostasis, contrary to Yu et al.' s (2010) results from Inner Mongolia grasslands. Currently, domestic research on how plant homeostasis affects plant growth and development and ecosystem structure mainly focuses on Inner Mongolia grassland ecosystems, with few reports on other ecosystems. Therefore, research should be strengthened across different ecosystem types and larger geographic scales to verify the universality of plant ecological stoichiometric homeostasis theory.

(2) **Physiological and ecological significance of plant stoichiometric homeostasis.** Plant stoichiometric homeostasis is closely related to plant adaptability and ecological strategies (Güsewell, 2005; Frost et al., 2005; Yu et al., 2010). Plants with strong homeostasis have conservative nutrient utilization strategies, maintaining slow growth even in barren environments, while low-homeostasis plants show greater adaptability. Homeostatic plants are adapted to stable environments, whereas low-homeostasis plants have advantages in variable environments (Persson et al., 2010). However, in-depth research is lacking on the mechanisms of plant homeostasis strength in response to environmental changes and ecological adaptation strategies. Therefore, further strengthening of physiological and ecological research on plant stoichiometric homeostasis is needed.

(3) **Relationship between plant stoichiometric homeostasis and growth rate.** Many studies have found that under relatively constrained biochemical allocation, algae may maintain N:P within a narrow range to meet rapid growth requirements, suggesting an intrinsic relationship between stoichiometric homeostasis and growth rate (Elrifi & Turpin, 1985; Shafik et al., 1997; Persson et al., 2010). Current research on vascular plants shows that at the species level, species with greater growth rate variation also show larger variation ranges in N:C, P:C, and N:P ratios, while species with smaller growth rate variation show smaller variation ranges in C:N:P ratios, possibly indicating a positive correlation (Yu et al., 2010, 2012). However, few studies in China have examined the relationship between plant stoichiometric homeostasis and growth rate, with scarce research achievements. Future studies should strengthen investigations of this relationship.

(4) **Stoichiometric homeostasis characteristics of special biological groups such as forest epiphytic plants.** Current ecological stoichiometric homeostasis research focuses primarily on marine organisms, terrestrial plants, and some wetland plants. Forest canopy epiphytes are an important and special plant group in mountain forest ecosystems. Unlike terrestrial plants, epiphytes lack roots connected to soil and absorb

nutrients and water primarily from the atmosphere. Are the results and theories obtained from terrestrial plant ecological stoichiometry applicable to epiphytes? How should the growth substrate be determined when calculating epiphyte stoichiometric homeostasis index H? How should homeostasis strength be evaluated? No related studies have been reported. Furthermore, the relationship between epiphyte stoichiometric homeostasis characteristics and canopy epiphytic subsystems or entire ecosystem structure, function, and stability represents new questions for plant ecological stoichiometry research, facing new challenges in research objects and methods. This area deserves strengthened research to further enrich the theory and methods of plant ecological stoichiometric homeostasis.

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Note: Figure translations are in progress. See original paper for figures.